

SPREAD-WING POSTURES AND THE WATER REPELLENCY OF FEATHERS: A TEST OF RIJKE'S HYPOTHESIS

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ABSTRACT.—Rijke (1967, 1968) proposed that the water repellency of feathers and the presence or absence of spread-wing postures in water birds could be explained by a structural mechanism first described for textiles. The textile model predicts that the tendency of water droplets to bead up on grid-like surfaces is a mathematical function in which the primary independent variable is an index, $(r + d)/r$, where r is the radius of and d is one-half the distance between cylinders in the grid. Larger indices indicate more water-repellent surfaces. Rijke found larger indices in the feathers of ducks than in the feathers of cormorants and anhingas; hence, he concluded that the latter birds must spread-wing to dry their wettable feathers. However, there were mathematical inconsistencies, undefined variables and concepts, and inadequate data in Rijke's papers. Despite these flaws, Rijke's hypothesis has been frequently cited in the ornithological literature. I report here my evaluation of the applicability of the textile model to feathers and my test of Rijke's prediction that species that assume spread-wing postures when wet have smaller $(r + d)/r$ values for their ramus and barbule structure than species that do not. I used scanning electron microscopy to measure the feather structure of 14 species of water birds in 6 different categories (breast, back, and four regions of a remex). I found that the textile-feather analogy is not realistic, because feather structure is considerably more complex and variable than the geometric model that is fundamental to the textile equations. My $(r + d)/r$ values show considerable overlap among three behaviorally distinct groups of water birds: those that predictably, occasionally, or never assume spread-wing postures. Statistically, the $(r + d)/r$ values of the rami in some feather categories of the group of species that shows spread-wing behavior were smaller than those of the other two groups of birds (which did not differ). Index values of the barbule structure, which constitutes most of the feather surface, however, do not differ significantly among the three groups of birds. I also measured the shape of water droplets (by contact angles) on the breast and remex feathers of a Mallard (*Anas platyrhynchos*) and a Reed Cormorant (*Phalacrocorax africanus*) and compared these values between the two species as well as with those mathematically predicted by the textile model. In general, the observed water droplets have a shape more like that predicted by the $(r + d)/r$ values of barbules than of rami. Droplets on the feathers of the Reed Cormorant were more bead-shaped than those on Mallard feathers, although the reverse should be true if the textile model holds for feathers. I conclude that Rijke's hypothesis is invalid for two reasons: the textile model cannot be applied reliably to feathers, and it does not account for the spread-wing behavioral differences among water birds. Received 12 April 1983, accepted 12 October 1983.

RIJKE (1967, 1968) published two nearly identical papers in which he proposed that a mathematical model derived to explain the water repellency of textiles could also resolve three ornithological issues: (1) the water repellency of feathers; (2) the absence of spread-wing postures in most species of water birds; and (3) the function of this behavior in cormorants and anhingas. Rijke's model provided a plausible answer to the paradox that Townsend (in Bent 1922: 241) pointed out: if spread-wing postures are necessary to dry the wings, why is the behavior not shown by water birds other than cormorants and anhingas? Hailman (1969a, b),

however, reviewed Rijke's papers (1967, 1968; hereinafter reference to Rijke refers to these years unless other dates are given) and pointed out several problems, most notably, several mathematical inconsistencies, an undefined variable, and an unsupported assumption. Despite these drawbacks, Rijke's conclusions have been generally accepted in the ornithological literature (see below).

Hailman recommended that I look into Rijke's papers when I was preparing a note on my field observation of an Osprey (*Pandion holiaetus*) performing spread-wing behavior (Elowson-Haley 1982). In doing so, I found several more

inconsistencies (detailed below) that prompted me to reevaluate the hypothesis with respect to issues (1) and (2) above. I present the results of that study in this paper. I have not considered here the function of spread-wing postures, which is a complex question that has been investigated elsewhere (Bernstein and Maxson 1982, Hennemann 1982, Winkler 1983, and the references therein).

Rijke based his hypothesis on a resemblance of feather structure to textile structure. The textile model (Cassie and Baxter 1944, Baxter and Cassie 1945) states that the water repellency of porous surfaces increases with the size of an index that is calculated from the dimensions of elements in the surface structure (i.e. the threads). Cassie and Baxter (1944) even suggested the applicability of their model to feathers, which may have motivated Rijke to test the idea. Using light microscopy, he measured the feather structure of seven species and found larger indices in ducks than in cormorants. Therefore, he concluded that cormorants, unlike ducks, have wettable feathers that require drying by spread-wing postures.

Rijke's work has been noted in the literature in two somewhat different contexts: feather structure determines its water repellency and the feathers of cormorants and anhingas are wettable. Some authors have cited the original textile papers (Cassie and Baxter 1944, Baxter and Cassie 1945) as having established the first concept (Thompson 1953; Kennedy 1970a, b, 1972; Rutschke 1976). Rutschke (1960) took measurements from mallard feathers and concurred with the estimates Cassie and Baxter (1944) gave. Many more authors, however, have cited Rijke's conclusions with respect to feather structure and water repellency (Clark 1969; Kennedy 1970b; Stettenheim 1972, 1976; Rutschke 1976; Rhijn 1977; Schreiber 1977; Jones 1978; Winkler 1983). Bernstein and Maxson (1982) discussed Rijke's conclusions in both contexts. Although they measured the feather elements of the Antarctic Blue-eyed Shag (*Phalacrocorax atriceps*) to contrast with Rijke's data for other species of cormorants, they noted Hailman's (1969a, b) objections to the model. Without reference to the underlying process, McAtee and Stoddard (1945) and Owre (1967) proposed that cormorants and anhingas have a wettable plumage or feather coat (nomenclature from Humphrey and Parkes 1959; the feather coat is the aggregate of feathers worn

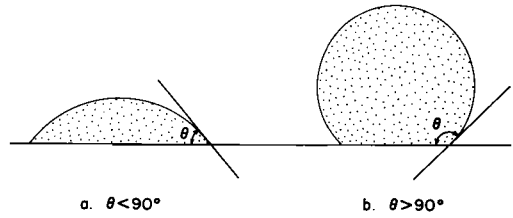


Fig. 1. Contact angles of water droplets resting on (a) wettable and (b) water-repellent surfaces.

by a bird at any given time). Despite the fact that Rijke did not evaluate the wettability of the feather coat as a whole, several authors have cited him as providing a mechanism that makes this suggestion plausible (Clark 1969, Kennedy 1971, Kahl 1971, George and Casler 1972, Siegfried et al. 1975, Mahoney 1981, Bernstein and Maxson 1982, Hennemann 1982). Finally, Kennedy (1969) has cited Rijke's work as having established a drying function for the spread-wing postures of cormorants and anhingas.

Neither Rijke's hypothesis nor my test of it is comprehensible without some explanation of the textile model itself. In what follows, I present that model followed by Rijke's data and finally the predictions that should hold if the hypothesis were true.

The textile model and feathers.—The distinction between "water-repellent" and "water-proof" surfaces needs clarification, as authors (Rowen and Gagliardi 1947, Crisp 1963) have pointed out multiple uses of the latter term. Truly waterproof materials, such as a yellow rain slicker, are almost impermeable to water. Water-repellent surfaces, by contrast, cause water to bead up and roll off under brief exposures in ordinary atmospheric conditions, but such surfaces will become wetted upon extended exposure or under increased pressure. Denim fabrics and feathers are water-repellent surfaces, and Rijke's model deals with repellency *per se*.

The textile model (Cassie and Baxter 1944, Baxter and Cassie 1945) is considered to be the state of the art for the water repellency of porous surfaces (Crisp 1963). The water repellency of a surface is determined by whether water droplets on it bead up (repellent) or flatten and spread out (wetable) (Fig. 1). Thus, surface wettability can be operationally expressed as the angle made by the surface and a tangent to a droplet's curvature at the point of contact,

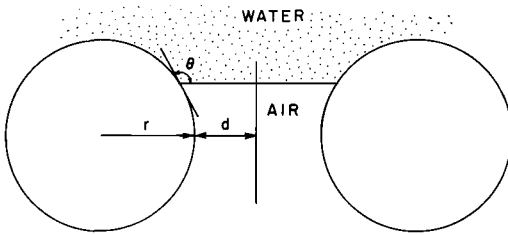


Fig. 2. Cross section of a pore covered by a water droplet many times larger in size; r is the radius of the cylinders and d is $\frac{1}{2}$ the distance between adjacent cylinders. θ is an angle used to derive f_1 and f_2 . (The meniscus of water is ignored.)

measured through the liquid (see Fig. 1). This is the contact angle θ ; it is *intrinsic* to the surface material. As Fig. 1 shows, larger angles describe more spherical droplets, and therefore, more water-repellent surfaces.

Cassie and Baxter (1944) showed that surface porosity changes the intrinsic contact angle to a larger effective contact angle (θ') because pores under the droplet add air spaces for which water molecules have little affinity. Cassie and Baxter termed the new angle the "apparent contact angle" (θ_A) and Rijke used this expression as well as "effective contact angle." I use the latter term.

Two kinds of intrinsic contact angles are important to Cassie and Baxter's (1944) equations. They can be visualized in rain drops individually trickling down a dirty window pane. The rounded advancing front of a droplet has a larger angle, the advancing contact angle θ_A (not to be confused with Rijke's effective contact angle θ_A). This advancing angle determines the penetration of water into porous surfaces such as feathers (Cassie 1948). The following tail of the droplet has a much smaller angle, the receding contact angle θ_R , that determines the water repellency of such surfaces. Rijke discussed intrinsic contact angles but did not differentially label them in his equations.

The structural factors in the textile equations describe the porous surface, which Cassie and Baxter (1944) illustrated as a cross section where a series of circles represent parallel cylinders (i.e. the threads) (Fig. 2). Specifically, these factors describe the areas of solid/water contact (i.e. on the cylinders) and air/water contact (i.e. over the pore) per unit planar area of surface

(see Fig. 2). Cassie and Baxter's (1944) mathematical statement for water repellency is:

$$\cos \theta'_R = f_1 \cos \theta_R - f_2, \tag{1}$$

where θ'_R is the effective receding contact angle on the porous surface; θ_R is the intrinsic receding contact angle on the same solid material as is in the porous surface, but smooth (i.e. not porous); and f_1 is an expression for the ratio of solid/water contact and f_2 for air/water contact. Thus, equation (1) is an expression for the shape of a water droplet on a porous surface caused by the affinity of the solid material for water (θ_R) and by the structure, or topography, of the surface (f_1 and f_2). From geometric properties of the structure, Cassie and Baxter (1944) derived the following equations for f_1 and f_2 :

$$f_1 = [\pi r / (r + d)] [1 - (\theta_A / 180^\circ)] \tag{2}$$

and

$$f_2 = 1 - r \sin \theta_A / (r + d), \tag{3}$$

where r is the radius of the cylinders, and d is one-half the distance between adjacent cylinders (see Fig. 2). θ_A is the intrinsic advancing contact angle made on a nonporous solid of the same material as is in the porous surface. The effective *advancing* contact angle θ'_A can be calculated by substituting θ_A for θ_R in equation (1). These equations, though not intuitive, have gained credibility by application in diverse disciplines (Disc. Faraday Soc. 1948, *Advances in Chem.* 1964, Moilliet 1963, and Zografis pers. comm.). Their derivations are available in the given references. Cassie and Baxter (1944: 549) showed that, if θ_A and θ_R are treated as constants, their model predicts larger θ'_R for larger values of $(r + d)/r$ (i.e. differently gauged grids of the same material). I term this expression the "structural index," or simply "index." Note that the index gives a dimensionless value.

The variable terms in the three equations are applied to feathers as follows. In a general sense, the elements of feather structure can be considered analogous to the parallel cylinders of the textile model (Fig. 2). The rami [nomenclature from Lucas and Stettenheim (1972); the barb is a primary branch, or ramus, plus its distal and proximal barbules] radiate from the rachis in approximately parallel rows. Between

adjacent rami are distal and proximal barbules each in roughly parallel rows that have varying angles with respect to the rami. Smaller feather elements such as barbicels do not contribute significantly to the feather/water surface. Therefore, the ramus or barbule radius is r and $\frac{1}{2}$ the distance between adjacent rami or barbules is d . Note that feather structure generates two indices, one for rami and another for barbules. The intrinsic contact angles θ_A and θ_R for feathers are those formed by water droplets on the feather rachis (nonporous surface).

Rijke's data.—Rijke tested one prediction—whether the $(r + d)/r$ values of the rami are larger in species that do not assume spread-wing postures (ducks) than in those that do (cormorants and anhingas). His results (Table 1), show that the indices of these behaviorally distinct groups can differ by as little as 1.0 (see Table 1, the difference between the data for the African Shelduck and Great Cormorant).

In addition to the problems Hailman (1969a, b) noted, Rijke's data are an inadequate test of his hypothesis for several reasons. First, they represent more than one feather type. He stated that the African Shelduck index was from wing-feather measurements and all of the other indices were from breast feathers. In a later footnote, however, Rijke (1970: 473) noted that the African Darter value (see Table 1) was for a quill (remex), and it should instead be listed as 11.0 for a breast feather. Second, Rijke contrasted the indices of five cormorant and anhinga species with only two anatid indices, which were from entirely different types of feathers. This is not compelling evidence that ducks do not adopt spread-wing postures because their larger structural indices confer upon them water-repellent feathers. Third, Rijke did not report where he measured on the feathers. This is an unfortunate omission, because the rami and barbules vary in cross section and distance apart within and among feathers and among species (Chandler 1916, Lucas and Stettenheim 1972, Stettenheim 1976). Therefore, r and d are variable within species, and the small numerical difference Rijke observed between ducks on the one hand and cormorants and anhingas on the other may be due to structural differences between feather types or regions and not taxonomic differences in structure. Fourth, the data in Table 1 are based on measurements of rami only. Because barbules com-

TABLE 1. Rijke's data (see text for details).

Species	$(r + d)/r$
Mallard (<i>Anas platyrhynchos</i>)	5.9
African Shelduck (<i>Tadorna cana</i>)	5.8
Reed Cormorant (<i>Phalacrocorax africanus</i>)	4.3
Bank Cormorant (<i>P. neglectus</i>)	4.5
Cape Cormorant (<i>P. capensis</i>)	4.4
Great Cormorant (<i>P. carbo</i>)	4.8
African Darter (<i>Anhinga rufa</i>)	4.5

prise a large portion of the feather surface, a credible test of structure-dependent water repellency should evaluate them as well. In sum, Rijke's data are not sufficient to support his conclusions, because they represent several feather types, have too few values for ducks, are not replicable, and do not contain barbule measurements.

Moreover, as Hailman (1969a, b) pointed out, Rijke did not present water repellency in operational terms. Rijke calculated the effective contact angles for only two species: 143° for the Mallard, which does not show spread-wing postures, and 121° for the African Darter, which does. In these calculations Rijke assumed without explanation that θ_A is constant at 90° and θ_R at 60°. Also, without explanation, Rijke (1968: 188) concluded that 121° "is too small to effect indefinite pearling off."

I calculated the θ'_R using Rijke's data and his values for θ_R and θ_A in equations 1–3 and found 134° for the Mallard and 127° for the African Darter. Hence, these species theoretically differ by 7°, not 22° as Rijke reported—not a large distinction. Possible differences in the water repellency of these two species are also confounded by the θ'_R calculated with the one barbule index Rijke gave: 4.7 for the Mallard. In this case, the θ'_R is 128°, very nearly that predicted with Rijke's data for the African Darter. Even more confusing is the angle calculated for the African Darter when Rijke's footnoted revision of its index changed from 4.5 to 11.0. Then this species has an θ'_R of 147°—larger than the duck. In sum, the outcome of Rijke's incorrect calculations and muddled data is the lack of an operational definition for feather water repellency.

Predictions.—If Rijke's hypothesis were true, then the $(r + d)/r$ values for rami of birds that

TABLE 2. Species for which ramus and barbule dimensions were measured.^a

Species	Spread-wing behavior ^b	References for behavior
Common Loon (<i>Gavia immer</i>)	N	Palmer (1962)
Pied-billed Grebe (<i>Podilymbus podiceps</i>)	N	Palmer (1962)
Reed Cormorant (<i>Phalacrocorax africanus</i>)	Y	Siegfried et al. (1975)
Double-crested Cormorant (<i>P. auritus</i>)	Y	Lewis (1929)
Anhinga (<i>Anhinga anhinga</i>)	Y	Clark (1969)
African Darter (<i>A. rufa</i>)	Y	Cramp and Simmons (1977)
Brown Pelican (<i>Pelecanus occidentalis</i>)	O	Schreiber (1977)
American White Pelican (<i>P. erythrorhynchos</i>)	O	Schaller (1964)
Magnificent Frigatebird (<i>Fregata magnificens</i>)	O	Cramp and Simmons (1977)
Mallard (<i>Anas platyrhynchos</i>)	N	McKinney (1965)
European Shelduck (<i>Tadorna tadorna</i>)	N	McKinney (1965)
White-winged Scoter (<i>Melanitta fusca</i>)	N	McKinney (1965)
Ruddy duck (<i>Oxyura jamaicensis</i>)	N	McKinney (1965)
Osprey (<i>Pandion haliaetus</i>)	O	Elowson-Haley (1982)

^a Measurements taken in each of six feather categories (see text).

^b Refers to assumption of spread-wing posture by wet birds: Y = predictably; O = occasionally; N = never.

predictably assume spread-wing postures when wet should be smaller than those of species that occasionally assume the posture, which, in turn, should be smaller than those of species that never show this behavior. The same prediction should also be true for indices of the barbules. Also, if the theoretical textile model is viable with respect to feathers, then calculated contact angles should predict those observed.

METHODS AND MATERIALS

Measurement of r and d.—I measured the ramus and barbule structure of 14 species in six feather categories: breast, back, and four areas of a primary (remex) (outer vane proximally and distally and inner vane proximally and distally). Unavoidably, the particular (number) remex I used varied from species to species. Table 2 lists the species and notes whether or not and how consistently they assume spread-wing postures, based on the literature listed. In addition to these species, I also studied the feathers of the Dipper (*Cinclus cinclus*) in all six categories. The barbule and ramus structure was so very different from the 14 nonpasserine species I studied, however, that it was not possible to measure the *r* and *d* dimensions, let alone contrast the indices of Dipper feathers to those of the other species.

I used scanning electron microscopy (SEM) to measure the feather elements, because I could not resolve them with light microscopy with either reflected or transmitted light. To prepare samples for SEM, I cut 1-cm² pieces from the feathers of one individual in each species, taking care to cut in corresponding places for all species. I mounted the uniquely numbered samples with the dorsal (i.e. outermost) side up on aluminum SEM stubs with double-stick tape.

Each stub was grounded with silver paint (#1481, Ernest F. Fullam, Schenectady, NY) and shaded with a 0.02–0.03- μ m-thick layer of 60% gold and 40% palladium in a vacuum vaporizer (Denton). I took micrographs at 100 \times with a Japan Electron Optics Laboratory SEM Model JSM-U3 fitted with a Polaroid camera using Polaroid Land 4 \times 5 film (Type 551 Positive-Negative).

On each micrograph, I outlined an area roughly parallel with and 400–500 μ m from the rachis and, with a metric rule, took 2 (when structures were so large as to preclude more) to 8 measurements of the rami and barbules (the latter at 50 μ m from the ramus). On most micrographs I could not measure both *r* and *d* at one spot, thereby finding its index. Therefore, the indices presented herein are calculated from the mean *r* and *d* values for each sample. As a measure of sample variability in the index, I found the maximum and minimum indices for each sample given all the possible (*r* + *d*)/*r* values from the separate (not mean) *r* and *d* measurements.

Measurement of contact angles.—I measured contact angles by the sessile drop method (Bigelow et al. 1946) with a special apparatus designed by B. Johnson (1982) and an optical system commercially available through Gaertner Scientific Corporation of Chicago, Illinois. The apparatus delivered water droplets of known volume onto feather samples (1 cm²) in a housing of constant temperature and humidity. After delivering a droplet of triple-distilled water, I allowed a 30-s equilibration time and then took 4–6 readings of the contact angle from each of the two visible sides of the droplet. As is standard with this technique, I considered the advancing angle to be that formed 30 s after delivery of the drop and the receding contact angle to be that formed 30 s after some of the liquid was removed. The feathers were not washed or treated before this procedure.

Due to my limited use of the apparatus, I was able to measure θ_A , θ_R , θ'_A , and θ'_R for only the following Mallard and Reed Cormorant samples (cut from areas contiguous with those used for the SEM work): the primary rachises (θ_A and θ_R only), the breast feather vanes; and the proximal primary inner vanes. I used the mean θ_A and θ_R values to calculate the predicted θ'_A and θ'_R for these two species.

Statistical analysis.—I used nonparametric tests to avoid making assumptions concerning distributions. I analyzed whether or not the structural index differed significantly among the three groups (see Table 2) of species with one-tailed Mann-Whitney *U*-Tests (Siegel 1956). Each analysis was a pair-wise comparison (within one feather category) with an H_0 such that the $(r + d)/r$ values did not significantly differ. The level of significance (α) was 0.05.

RESULTS

The feather/textile analogy.—Figure 3 presents micrographs of the 6 feather categories for 3 species, representing the 3 behavioral groups listed in Table 2. In all but two micrographs, the widest elements are rami, and the numerous smaller elements are barbules (BK and BR in group B are the exceptions, where the widest element in each is the rachis). Note that barbules constitute most of the feather surface area.

With respect to the feather/textile analogy, Fig. 3 indicates that feather structure is much more complex than the ideal porous surface shown in Fig. 2. Note that the distal barbules branching from one ramus often cover the distally adjacent ramus—covered rami cannot contribute to superficially determined water repellency. The micrographs reveal that the shape of the rami varies (see especially groups A and B) from somewhat flattened in the proximal primary (POV and PIV) to somewhat rounded on the distal primary (DOV and DIV). Therefore, the r value of a ramus varies over the feather surface. The d dimensions of rami are also highly variable, especially on the primaries (contrast the outer and inner vanes in any one row of micrographs). Stettenheim (1976) has likewise commented that the rami of a feather vary in their angle of attachment to the rachis. Figure 3 also reveals that the barbules do not have the uniform structure fundamental to the textile model. Note that the barbule d distances in the breast and back feathers of all three species vary considerably.

The variability of r and d within and among feather types or regions of a given species is

also apparent in their mean values (presented in the Appendix). For example, in the Pied-billed Grebe contrast the r values for the rami in distal primary outer and inner vanes—11.65 μm to 22.50 μm , respectively. Also, the d values for the rami in the Mallard proximal primary remiges vary from 86.67 μm on the outer vane to 145.00 μm on the inner vane. Lucas and Stettenheim (1972: 259) reported equal or greater variation within the same vane.

In addition to supporting my view that the structural difference Rijke observed may be due to differences among feathers and not among taxa, the variability of structure evident in the micrographs and Appendix data challenge Rijke's hypothesis for another important but subtle reason. The model assumes parallel rows of perfect cylinders, because the equations for f_1 and f_2 are derived from a geometric analysis of the diagrammatic model in Fig. 2. Because feather structure does not reasonably conform to this physical model, however, the reliability of the textile equations in predicting its contact angles, hence water repellency, is in doubt.

Index differences in relation to spread-wing behavioral differences.—The $(r + d)/r$ values I calculated from the SEM measurements are presented in Fig. 4. The figure is relatively complex and requires a few notes of explanation. Indices from the 4 primary and 2 body contour feather categories are presented for all species in blocks (a) to (f). The species are grouped (indicated by stripes, stipples, or clear) according to their spread-wing behavior as indicated in Table 2. Superimposed on the data for the rami are dashed and solid lines that correspond respectively to Rijke's largest index for a species with reputedly wettable feathers and to his smallest index for a species with reputedly water-repellent feathers. The range indications at the end of each bar designate the maximum and minimum $(r + d)/r$ values given the variability of r and d in each micrograph.

Consider first Rijke's delimiting values indicated by the dashed and solid lines. Note that for many species my data do not consistently support his water repellent/wettable dichotomy. For example, the indices of the rami in the proximal primary remiges of the Mallard, European Shelduck (both, for outer vane data, Fig. 4b), and the Ruddy Duck (inner vane, Fig. 4a) are within the range of those Rijke reported as causing wettable feathers, yet these species do not assume spread-wing postures. Further-

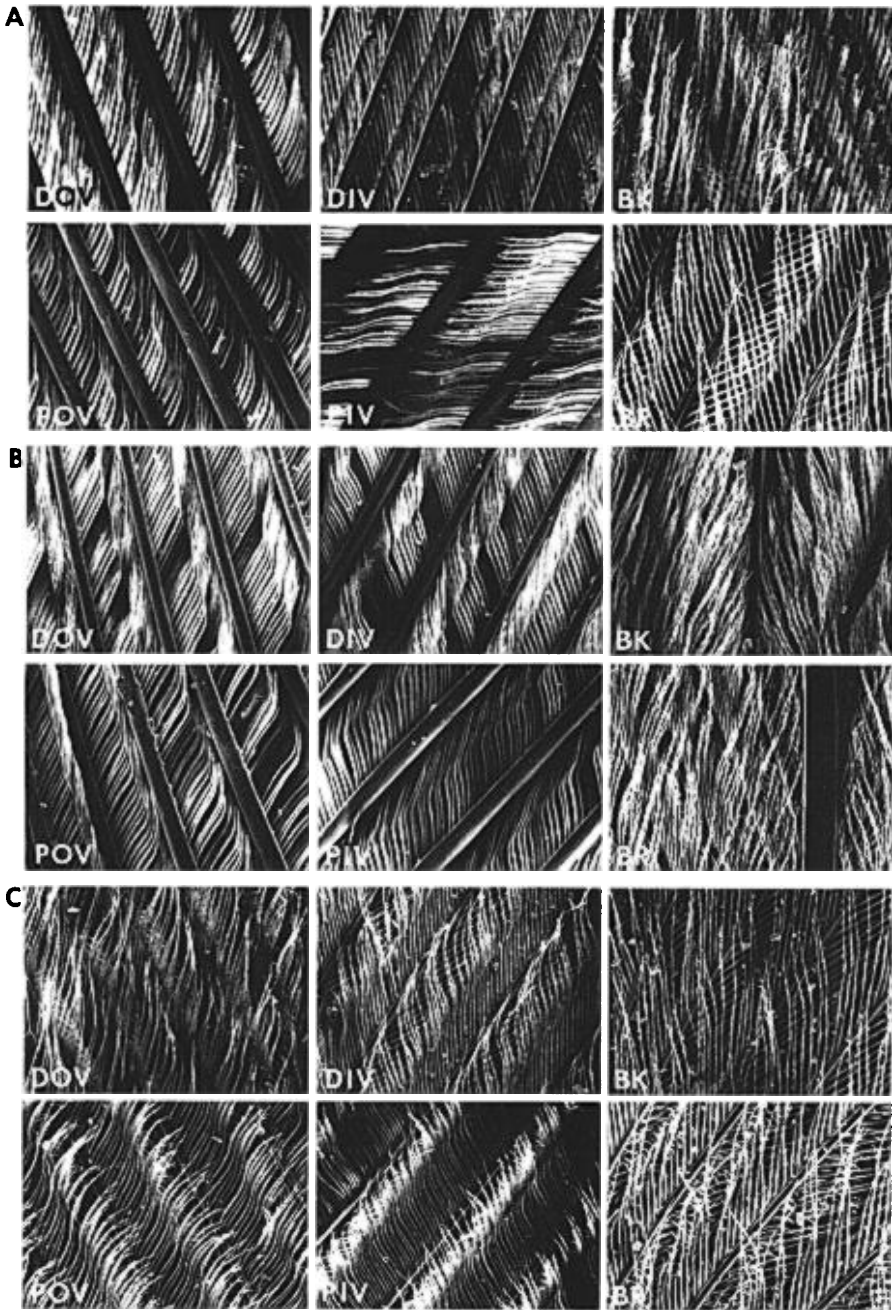


Fig. 3. SEM micrographs (100 \times) of the six feather categories from three species (see Table 2 as to their spread-wing behavior): (A) Reed Cormorant, (B) Brown Pelican, and (C) White-winged Scoter. The feather categories are: DOV, distal primary outer vane; DIV, distal primary inner vane; BK, back; POV, proximal primary outer vane; PIV, proximal primary inner vane; and BR, breast. All the micrographs show the dorsal surface of the feather samples, which are oriented with their distal end uppermost on the page.

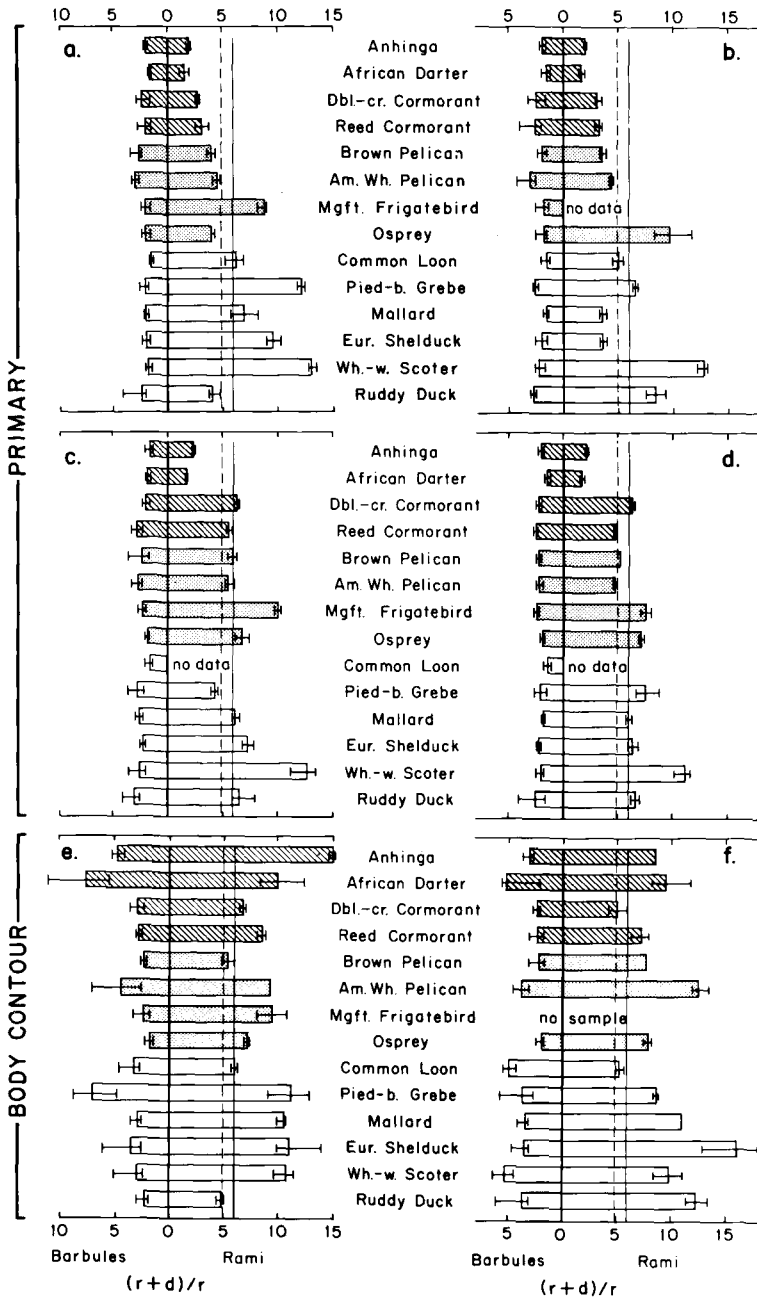


Fig. 4. The index for rami and barbules (respectively right and left of the heavy lines at (0) based on SEM measurements. The six feather categories are: (a) PIV, (b) POV, (c) DIV, (d) DOV, (e) breast, and (f) back. For further explanation, see text and legend to Fig. 3.

TABLE 3. Probabilities from pair-wise one-tailed Mann-Whitney *U*-tests of $(r + d)/r$ values for the rami.

Feather categories	Pairs of bird groups compared ^a		
	Y/N	Y/O	N/O
Breast	NS ^b	NS	NS
Back	(NS) ^c	NS	NS
Primary ^d			
DIV	(NS)	NS	NS
DOV	0.032	NS	NS
PIV	0.005	0.014	(NS)
POV	0.005	0.028	NS

^a Y = species that predictably spread-wing; O = species that occasionally spread-wing; N = species that never spread-wing.
^b NS = not significant ($P > 0.05$).
^c (NS) = Not significant, but $0.06 > P > 0.05$.
^d DIV, DOV, PIV, POV as defined in legend to Fig. 3.

TABLE 4. Probabilities from pair-wise one-tailed Mann-Whitney *U*-tests of $(r + d)/r$ values for the barbules.

Feather categories	Pairs of bird groups compared ^a		
	Y/N	Y/O	N/O
Breast	NS ^b	(NS) ^c	NS
Back	NS	NS	NS
Primary ^d			
DIV	NS	NS	NS
DOV	NS	NS	NS
PIV	NS	NS	(NS)
POV	NS	NS	NS

^a For key see Table 3.
^b NS = not significant ($P > 0.05$).
^c (NS) = not significant, but $0.06 > P > 0.05$ (but see text).
^d Categories as defined in legend to Fig. 3.

more, the data for the distal primaries show that the Double-crested Cormorant has a larger ramus index, therefore supposedly *more* water-repellent feathers, than does the Pied-billed Grebe, when their inner vane data are compared (Fig. 4c); yet the opposite is true of the data for their outer vanes (Fig. 4d). Finally, note that Rijke's distinction between "water repellent" and "wettable" indices is meaningless when applied to the data on the breast and back feathers.

The results of Mann-Whitney *U*-tests on the data for the rami in Fig. 4 are presented in Table 3. Of 18 comparisons, only five supported Rijke's conclusion by rejecting the null hypothesis. These results are not clear-cut, but they suggest that his hypothesis may be valid to the extent that the primaries of ducks have a ramus structure that is theoretically more water repellent than those of aningas and cormorants. It is puzzling that Rijke reached this conclusion almost entirely on the basis of breast feather indices, which do not differ significantly among the three groups of birds.

Rijke did not measure barbule structure or define its relative water repellency in terms of $(r + d)/r$ values. It is reasonable to assume, however, that the same delimiting values he found for the rami should also characterize the wettable/water repellent dichotomy of the $(r + d)/r$ data for barbules. With this perspective, note that, with a few exceptions in the breast and back feather data, the indices of barbules are all smaller than 4.8. By Rijke's criteria, 4.8 is too small to generate the large effective contact angles of beaded droplets. Therefore, based on barbule structure, all 14 species of this

study have "wettable" primaries and most have "wettable" body feathers.

My statistical analysis of the $(r + d)/r$ data for barbules (Table 4) overwhelmingly rejects Rijke's hypothesis. Although two comparisons gave equivocal results (see Table 4), these do not even weakly support Rijke's hypothesis, because in both cases the indices that should have been the smallest (i.e. of species that perform spread-wing postures) were in fact the largest and vice versa. The lack of any significant difference in the indices of barbules among the three groups of species is all the more compelling, because the barbules contribute far more surface area than the rami.

Calculated and observed effective contact angles.—Do the textile equations accurately predict the measured water repellency of feathers, as Rijke implicitly assumed? The observed values for contact angles on the feather samples from a Reed Cormorant and a Mallard (Table 5) provide some insight into this question. I solved for the calculated angles by using the indices given in Fig. 4 for the two species and the mean values for θ_r and θ_A given in Table 5. The observed angles are not differentiated as to rami and barbules, because the droplets covered both. If Rijke's assumption is correct, there should be good agreement between the observed and calculated angles.

Consider, first, angles calculated with indices of the rami. In the Mallard, the observed θ'_A and θ'_R on the sample from the breast feather differed from those predicted by 17° and 29°, and the observed/predicted θ'_{RS} for its primary remex differ by 24°. These are large differences—in the range of that which Rijke saw as distinguishing between species with putative

TABLE 5. Comparison of observed and calculated advancing and receding effective contact angles.^a

Species	Feather	Calculated θ'_A		Observed angles		Calculated θ'_R	
		Ramus	Barbule	θ'_A	θ'_R	Ramus	Barbule
Mallard ($\theta_A = 88^\circ$, $\theta_R = 75^\circ$)	Breast	154°	130°	137°	121°	150°	121°
	PIV ^b	148°	117°	139°	119°	143°	105°
Reed Cormorant ($\theta_A = 95^\circ$, $\theta_R = 82^\circ$)	Breast	154°	134°	133°	130°	149°	126°
	PIV ^b	137°	124°	155°	146°	128°	113°

^a All observed angles are mean values.

^b PIV = proximal primary inner vane.

water-repellent or wettable feathers. The calculated and observed θ'_A s on the Mallard primary, differing by 9°, are perhaps in the range of agreement. The data for the Reed Cormorants also showed little agreement; the difference between the observed and calculated angles for both breast and remex feather samples was 18°–21°.

For the angles calculated with indices of the barbules, the breast and primary feather samples of both species show conflicting results. On the one hand the calculated and observed angles for the breast feathers of both species are in good agreement, differing by no more than 7°. On the other hand, however, the primary feather angles differed by 14°–33°, similar to the disparities found for the data of the rami.

Aside from the contrast between the observed angles and those predicted by Cassie and Baxter's equation, the data in Table 5 contradict Rijke's hypothesis for two reasons. First, recall that Rijke stated that an θ'_R value of 121° (for the African Darter), was too low to cause water droplets to pearl-off. Yet, the observed θ'_R s of the Mallard are 121° and 119° (see Table 5). These data, indicate that either Rijke's delimiting angle is incorrect or the textile model does not reliably describe water repellency in feathers. Second, under Rijke's hypothesis, the observed θ'_R and θ'_A of the Reed Cormorant should be smaller than those of the Mallard. Yet, comparing the angles on equivalent samples from the two species reveals, with one exception, that the Reed Cormorant angles are the larger. The exception is the breast feather θ'_A , the Mallard angle being larger by 4°. If cormorants are more wettable than ducks, these data suggest that the reason does not lie in the shape of water droplets on their feathers.

DISCUSSION

Rijke's application of the textile model is unrealistic for reasons over and above variable

structure and lack of agreement between predicted and observed effective contact angles. First, the equations that Cassie and Baxter (1944) derived and Rijke applied assume forces such as gravity or hydrostatic pressure to be negligible. As Crisp (1963) correctly pointed out, however, the ability of a porous surface to resist water penetration under external pressure is inversely proportional to the first power of scale size of the pores. This factor is insignificant at the water's surface, but pressure increases with depth. At only 10 m below the surface, a diving bird experiences an external pressure of 1 atmosphere relative to the surface. I question whether the textile model can reliably predict a difference in the potential wettability of the feathers on, say, a Common Loon and Double-crested Cormorant, both at 10 m underwater.

Second, the equations overlook an inherent difficulty in dealing with receding contact angles. These angles cannot be predicted reliably, because their size is affected by minute accumulations of water in surface pores and irregularities as the water droplet advances over that surface (Cassie 1948, Crisp 1963). For this reason, equation (1) is not a statement of the value of θ'_R , but of one in a range of possible values. Moreover, the accumulations of water can increase during prolonged immersion such that the effective receding angle may be considerably reduced. This phenomenon can be accelerated by immersion under pressure (Cassie 1958: 167). Considering these effects, the relevance of the textile water-repellency model to birds that dive and swim under water is doubtful.

Third, Rijke explicitly assumed that the secretions of the uropygial gland are neither extraordinary in waterproofing characteristics nor sufficiently variable among birds to account for species differences in water repellency. Although he later conceded (Rijke 1970: 471) that "the function of the gland oil necessarily in-

volves, besides lubrication, the basis for a finite contact angle," Rijke remained convinced that the water repellency of birds is primarily dependent upon the structural indices of their feather elements. Although the studies by Madsen (1941) and Fabricius (1959) support Rijke's view (based on their uropygial gland extirpation experiments), Stettenheim (1972) has stressed that they overlooked two possibilities: that a thin film of secretion remains on the feathers for some time and that the intrinsic feather lipids themselves are a possible factor in water repellency. Elder (1945) considered the gland essential to the water repellency of the feathering, and this seems likely given Langmuir's (1919, Zisman 1964) conclusion that a fatty acid monolayer on a surface considerably alters its wetting characteristics.

Despite their apparent agreement, there is an important distinction between Madsen's (1941) and Fabricius' (1959) conclusions and Rijke's point of view. The former were both attempting to explain the water repellency of the feather coat, not of individual feathers as was Rijke. It seems reasonable to me that characteristics of the entire feather coat would influence how wet a bird gets. The feather coats of ducks differ strikingly from those of cormorants and anhingas in their greater thickness. Moreover, there may also be differences among these birds in the density, distribution, and extent of overlap of their feathers, as well as whether or not there is laminar or turbulent flow around some areas of the submerged feather coat. Therefore, if cormorants and anhingas are wettable, it may be due to the architecture of their feather coats and not so much that of their feathers.

CONCLUSION

I reject Rijke's hypothesis that the textile model can explain the mechanism of water repellency in feathers and, as a consequence, resolve the question of why spread-wing postures are performed by cormorants and anhingas and not by other water birds. The textile equations are inappropriate for feathers, because their fundamental ideal model is inadequate to describe feather structure. My results show that the textile model fails to predict which species spread-wing and which ones do not. I found few significant differences among the $(r + d)/r$ values for the rami of species that predictably, occasionally, or never show the

behavior when wet. More important, indices of the barbules, which constitute more of the surface area than rami, show no significant differences among these groups of birds. Moreover, even with empirically measured values for the variables, Cassie and Baxter's (1944) equations do not consistently predict the observed effective contact angles on feathers. That is not to say, however, that feather structure is not a relevant factor in the water repellency of the feather coat—Rijke's approach is useful in promoting this issue, but his hypothesis does not provide the mechanism.

Finally, Rijke's conclusion that wing-drying is the function of spread-wing postures in cormorants and anhingas is based on an *a priori* assumption that the behavior serves only one function. Most certainly this is an oversimplification.

ACKNOWLEDGMENTS

Financial support came from the University of Wisconsin Graduate School and the Department of Zoology Davis Fund. I thank the Department of Zoology Museum staff for providing skins and the Department of Entomology for use of their SEM facility. I gratefully acknowledge the skill of Cheryl Hughes and Donald Chandler, who assisted with illustrations. G. Zografis and his student Barbara Johnson of the University of Wisconsin School of Pharmacy kindly let me use their contact angle equipment. I especially thank R. Schreiber of the Los Angeles County Natural History Museum for supplying me with feathers. I thank S. Kolmes, J. R. Baylis, and especially J. P. Hailman for helpful advice. I am grateful to P. Stettenheim, O. Owre, and an anonymous reviewer, all of whom contributed to an improved manuscript. Last, I thank my family for their unflinching support and patience.

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APPENDIX. Mean of *r* and *d* measurements (μm) for rami and barbules of the six feather categories studied.

	Proximal primary												Distal primary											
	Breast				Back				Inner Vane				Outer Vane				Inner Vane				Outer Vane			
	Rami	Barbules	<i>r</i>	<i>d</i>	Rami	Barbules	<i>r</i>	<i>d</i>	Rami	Barbules	<i>r</i>	<i>d</i>	Rami	Barbules	<i>r</i>	<i>d</i>	Rami	Barbules	<i>r</i>	<i>d</i>	Rami	Barbules	<i>r</i>	<i>d</i>
Common Loon	19.69	98.34	3.22	7.25	29.44	128.34	2.50	9.59	21.50	114.17	5.00	2.40	25.00	101.67	5.20	2.69	no data	4.75	2.70	no data	5.25	2.04		
Pied-billed Grebe	21.10	215.00	5.00	30.25	22.50	175.00	4.75	12.71	7.50	84.06	3.74	4.13	11.25	62.92	3.57	5.96	22.50	75.06	2.82	5.00	11.65	76.65	4.05	4.05
Reed Cormorant	17.50	131.25	5.00	9.38	15.94	100.00	5.83	7.00	47.00	101.25	4.35	4.17	30.25	69.06	3.96	6.25	19.38	88.75	4.38	7.44	22.92	87.92	3.75	5.50
Double-crested Cormorant	15.63	90.63	3.42	6.66	20.00	81.25	3.96	5.10	63.34	108.34	3.39	4.92	62.50	133.34	3.07	4.46	20.42	107.50	4.35	4.40	22.50	120.42	3.75	4.54
Anhinga	11.45	160.00	3.30	12.18	15.00	175.00	3.92	8.08	122.50	115.00	5.00	4.50	81.65	84.15	5.50	4.35	85.00	111.25	6.49	4.14	79.38	95.42	5.25	5.96
African Darter	20.42	181.67	2.50	16.56	15.69	134.17	5.00	20.84	145.63	68.75	5.32	3.27	73.75	49.50	5.28	2.60	99.48	72.19	5.60	4.50	75.63	57.50	5.35	2.65
American White Pelican	15.00	125.00	2.49	8.44	10.00	115.00	2.50	6.88	32.08	112.48	3.75	6.82	25.63	87.64	3.32	7.07	24.07	108.34	3.57	6.25	22.22	84.17	3.48	4.16
Brown Pelican	13.75	60.63	3.30	4.41	8.30	56.25	3.22	3.75	32.90	100.84	3.66	5.75	30.00	77.50	4.10	3.80	19.75	95.32	2.98	4.30	20.00	82.50	3.57	4.50
Magnificent Frigatebird	18.23	155.54	5.00	7.19	—	no sample	—	—	22.50	179.38	5.00	5.28	—	246.88	5.40	4.06	22.50	201.67	5.00	6.62	26.59	173.75	5.00	7.14
Mallard	10.00	96.25	4.40	8.51	10.00	100.00	3.53	8.44	24.17	145.00	5.00	4.59	34.85	86.67	5.54	3.12	13.33	69.17	3.30	4.95	12.92	65.63	3.60	2.50
European Shelduck	9.25	93.33	3.75	9.25	5.42	80.84	3.33	8.02	14.22	122.50	3.29	2.99	42.91	110.00	5.00	5.00	14.18	89.00	2.50	3.00	15.13	80.00	2.60	3.08
White-winged Scoter	13.60	132.09	3.32	6.53	11.04	98.34	1.65	7.01	10.00	121.67	4.90	3.42	10.00	117.17	4.05	5.00	10.33	120.00	2.82	4.46	7.92	80.00	3.10	3.33
Ruddy Duck	15.00	55.83	3.88	5.33	10.00	113.33	3.33	8.75	23.33	74.17	2.29	3.13	9.38	68.44	2.50	4.38	12.25	68.13	2.28	4.75	10.00	56.25	2.29	3.58
Osprey	12.50	78.33	3.42	2.57	15.00	105.00	4.80	3.82	48.34	150.00	5.00	4.79	18.13	157.50	5.00	3.93	22.50	130.00	5.00	4.30	28.75	177.50	5.00	4.33